

ON THE ECONOMICS OF BIOLOGICAL INVASION: AN APPLICATION TO RECREATIONAL FISHING

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ABSTRACT. The paper demonstrates four general mechanisms that may affect economically valuable species when exposed to biological invasion. We distinguish between an *ecological level effect* and an *ecological growth effect*. In addition, we present an *economic quantity effect* working through demand. Finally, we suggest that there is an *economic quality effect* that reflects the possibility that invasions affect the harvesting agents directly through demand-side forces. For example, this may occur because the state of the original species or the ecosystem is altered. We depart from the existing literature by revealing ecological and economic forces that explain why different agents may lack incentives to control invasions. The theoretical model is illustrated by the case where escaped farmed salmon (*EFS*) influence wild Atlantic salmon fisheries.

KEY WORDS: Biological invasion, escaped farmed salmon, recreational fishing, bioeconomic model.

1. Introduction. During the last few decades, there has been increasing concern about invasive species in various ecosystems. Holmes [1998] argued that invasive alien species are the second most important cause of biodiversity loss worldwide, beaten only by habitat degradation. In some instances, invasive species are introduced to a new environment in order to obtain some recreational or commercial gain. Perhaps the most famous case is the release of 24 wild rabbits by Thomas Austin for sport hunting on his property in Australia in 1859, which had far-reaching consequences (Williams et al. [1995]). In other instances, human activity indirectly has allowed intruders to establish themselves in a new environment by disturbing the natural balance in the environment, for example, via pollution. In addition, humans have accidentally brought invasive species to new places as stowaways in cargos. One well-known example is the Zebra mussels from the Caspian

Sea that were introduced to the Great Lakes in the USA via ballast water from a transoceanic vessel in the 1980s (Great Lakes Science Center [2000]). Although the economic consequences of nonindigenous species are recognized as important, there have been few attempts to quantify them. This is due to a lack of good data, as well as uncertainties and measurement problems when facing the many components that are difficult to quantify accurately (Perrings et al. [2000]). One exception is Pimentel et al. [1999], who estimated total economic damages and associated control costs due to invasive species in the USA to be \$138 million per year.

Several authors in Perrings et al. [2000] dealt with the economics of biological invasions. A general model formulation was given in Barbier [2001]. As in Knowler and Barbier [2000], the focus was on separating the *ex post* and *ex ante* economic consequences of biological invasions. Knowler and Barbier studied the introduction of comb jelly (*Mnemiopsis leidyi*) in the Black Sea and its impact on the commercial Black Sea anchovy fishery. Knowler et al. [2001] examined the extent to which pollution control could have prevented the ecological regime shift imposed by the comb jelly. Higgins et al. [1997] investigated alternative responses to the invasion of a woody species that has displaced a native plant species in a situation where both species are valuable. Settle and Shogren [2002] developed a general model to study the introduction into Yellowstone Lake of exotic lake trout, which pose a risk to the native cutthroat trout. In their model, the park manager, operating as a social planner, divided the budget between controlling the lake trout and an alternative service, the improvement of a nonspecies good. By contrast, humans divided their time into either species consumption or spending leisure time on a nonspecies composite good. Knowler and Barbier [2005], Eiswerth and van Kooten [2002], Horan et al. [2002], Olson and Roy [2002], and Shogren [2000] studied uncertainty with respect to species invasion. Several authors, including Buhle et al. [2004] and Hill and Greathead [2000], studied cost effective control. In a joint TC-CV study, Nunes and van den Bergh [2004] explored the extent to which people value protection against exotic species.

In this paper, we analyze yet another potential concern, namely the influence escaped farmed species may have on the natural habitants. More specifically, we study the effects that escaped farmed salmon (*EFS*) may have on wild Atlantic salmon (*Salmo salar*). The invaders

can be viewed as biological pollution, and in that sense, the paper is essentially an extension of McConnell and Strand [1989]. They analyzed the social returns to commercial fisheries when water quality influenced both demand and supply of commercial fish products under both open access and when fish stocks were efficiently allocated. The invasion case considered here requires additional demand and supply effects to be considered.

EFS (both Pacific and Atlantic salmon) is of great concern in a number of countries with fish farming industry, for example, United Kingdom, Scotland, Ireland, Iceland, Chile, USA, and Canada. In addition, the increasing farming of other fish species, such as cod, halibut, clams, and crabs, highlights the importance of addressing this issue. The farmed salmon's share of the world production of salmon increased from 2% in 1980 to 54% in 1999 (Bjørndal and Aarland [1999]). The bioeconomics of the interrelation between aquaculture and fisheries is studied by Anderson [1986], Ye and Beddington [1996], and Hannesson [2003], and market interactions are studied by Anderson [1985], Anderson and Wilen [1986], Asche et al. [2005], and Sumaila et al. [2007].

Norway has been the world leader in farmed salmon since this technique was pioneered in the late 1960s and production has risen steadily from 600 tons in 1974 to about 500,000 tons today (Bjørndal [1990], Statistics Norway [2004]). Salmon farming is therefore one of the most, if not the most, important industries in rural Norway today, with a yearly landing value of about NOK 10 billion (1.3 billion EUR). However, since the very beginning of the salmon farming industry, salmon have unintentionally escaped from net pens that are damaged by storms, seals, and otters, or by daily wear and tear. The number of accidental escapes decreased in the mid 1990s because of safety investments in the sea ranches. Nevertheless, approximately 400,000 salmon still escape yearly from fish farms in Norway (Table 1), a number exceeding the average total wild spawning stock (NOU [1999]).

The wild Atlantic salmon stock is traditionally harvested in two different fisheries in Norway during its spawning run. First, the marine commercial fishery catches about 40% of the spawning biomass in fishnets in the fjords and inlets. The remaining stock enters the rivers and is exploited by a recreational fishery. When the fishing season in the river closes, the remaining stock takes part in the reproduction process in the river in the late autumn.

TABLE 1. Escaped farm salmon (*EFS*) in Norwegian fisheries and river spawning stocks, 1989–2003.

Year	Total number of <i>EFS</i> (in 1,000)	<i>EFS</i> share of total catch in river fishery (%)	<i>EFS</i> share of total catch in marine fishery* (%)*	<i>EFS</i> share in spawning stock (%)
1989	—	7	30	35
1990	—	7	32	34
1991	—	5	30	24
1992	—	5	33	26
1993	498	5	34	22
1994	536	4	28	22
1995	240	5	28	29
1996	417	7	32	31
1997	506	9	40	29
1998	553	9	38	22
1999	348	6	33	15
2000	276	7	24	11
2001	272	7	23	11
2002	475	16	31	18
2003	240		18	13
Average, 1989–2002	412	7	31	24

Source: <http://www.miljostatus.no/templates/PageWithRightListing—2236.aspx>

*Un-weighted average, coast+ fjord.

Spawning *EFS* may have a number of negative effects on the natural growth and economic value of wild salmon. The most important effects are the spread of diseases and the mixing of genes through interbreeding, which affect the reproduction rate as well as the intrinsic value of the wild salmon (McGinnity et al. [2003], Fleming et al. [2000]). Farmed salmon dig in the natives' spawning gravel, get more aggressive and risk willing offspring (NOU [1999]), and increase the sea lice

density (Grimnes et al. [1996]). However, *EFS* may also have positive effects. Farmed salmon can potentially increase the salmon stock available for both marine and recreational catches, *ceteris paribus*, and thus improve the profitability of these fisheries. As reported in Table 1, *EFS* constitute a substantial part of the catch. This is not to say that invasion is no problem for the society as a whole, but it may reveal economic forces inducing lack of incentives for different agents to control the invasion. These mechanisms are ignored in the previous literature.

The analysis in this paper differs from the previous studies by Knowler and Barbier [2000] and McConnell and Strand [1989] in various ways. First, the model formulation is more general than Knowler and Barbier as it encompasses different *ex post* effects of invasions. Knowler and Barbier [2000] stressed the importance of comparing the *ex ante* with the *ex post* invasion case. We distinguish between changing ecological and economic forces, which have potentially different effects depending on the initial state. The constant ecological structural shift proposed by Knowler and Barbier [2000] is replaced by a shift that depends on the magnitude of the invasive influx.

Second, the general problem of invasion as a result of accidental releases from fish farms raises some specific new problems that have not yet been considered, for instance in the pollution framework of McConnell and Strand [1989]. We address one of these problems by explicitly taking into account the potentially ambiguous effect of biological invasion through demand-side effects.¹ In many respects, it may be impossible for the different harvesters to separate the wild and escaped species that they catch. Hence, if invasion increases the total stock, demand may increase due to what will be called the *economic quantity effect*.² However, it is relatively easy to discover whether there are genetic differences or variations between the wild and the reared species through genetic investigation. Hence, knowledge about the composition of the catch, as well as the composition of the breeding stock, is often available. Thus, harvesters know the likelihood of getting a farmed instead of a wild salmon. Furthermore, harvesters may be concerned about the health of the wild stock due to crossbreeding when the share of invasive salmon in the breeding stock is high. This could be related directly to the existence value of the genetically wild species or to the loss of biodiversity due to gene flow from the reared to the wild species. Another interpretation is that harvesters simply prefer to

harvest “clean” or “pure” wild Atlantic salmon. This will be called the *economic quality effect*. These two effects both influence the economic equilibrium condition.

Next, on the ecological side there are two effects as well: the *ecological growth effect*, which is negative, and the *ecological level effect*, which is positive. In the specific case of *EFS*, the former effect reflects a general decrease in the growth rate of the wild salmon due to crossbreeding (McGinnity et al. [2003], Fleming et al. [2000]), whereas the latter reflects the yearly influx of escaped salmon that add to the total salmon stock (see below).³ Analogous to the economic effects, these ecological effects affect the ecological equilibrium condition. Note that the *ecological growth effect* is analogous to the supply effect in McConnell and Strand [1989], while the *economic quality effect* is analogous to their demand effect.

We also consider measures to change the composition of catches in the marine and river fisheries. More specifically, we analyze the consequences of a sea fishing ban. It is often argued that a sea fishing ban increases the overall profitability in salmon fisheries because the value of a sea-caught salmon is more or less directly related to the meat value, whereas a river-caught salmon exceeds the meat value by several times (see Skonhøft and Logstein [2003]). When the composition of the catch, in terms of the share of the invasive species, differs between the various harvesters, we gain an additional management tool. By altering the share of the total catch between the different harvesters, the composition of the stock changes (Section 5.2).

The rest of the paper is organized as follows. Section 2 formulates an ecological model for the Atlantic salmon species, and section 3 defines the ecological equilibrium. In section 4, the economics of the river fishery are examined and the economic as well as the bioeconomic equilibrium conditions are defined. Next, in section 5, the model is illustrated by utilizing data from the Norwegian river Orkla. Section 6 concludes the paper.

2. The ecological model. First, we consider a wild fish stock in the absence of escaped farmed salmon. The size of the wild population in biomass (or number of fish) at the beginning of the fishing season in year t is X_t . Both a marine and a river fishery act on the

salmon during the spawning run from its offshore environment to the coast, where reproduction takes place in its parent or “home” river. The marine fishery impacts on the stock first because this harvest takes place in the fjords and inlets before the salmon reaches their spawning river (see Figure 1). For a marine exploitation rate $0 \leq h_t < 1$, the number of wild fish removed from the population is $h_t X_t$. Accordingly, the stock entering the home river is $(1 - h_t)X_t = S_{1,t}$. The river recreational fishery exploits this spawning population along the upstream migration. When the river exploitation rate is $0 < y_t < 1$, the spawning stock becomes $(1 - y_t)(1 - h_t)X_t = (1 - y_t)S_{1,t} = S_{2,t}$. This spawning stock hence yields a subsequent recruitment $R(S_{2,t})$ to the stock in year $(t + \tau)$, where τ is the time lag from spawning to maturation age (see e.g. Walters [1986])⁴. Throughout the analysis, it is assumed that the stock-recruitment relationship $R(\cdot)$ is of the Shepherd type, with $R'(\cdot) \geq 0$, $R''(\cdot) \leq 0$ and $R(0) = 0$ (more details below). We assume that none of the spawners survive.⁵ Therefore, the stock growth reads $X_{t+\tau} = R(S_{2,t})$ when there is no invasion.

The influx of *EFs* into the ecosystem, X^F , is a yearly event. As the influx is due to unintentional releases from the fish farms, it is exogenous and not subject to an equation of motion.⁶ As already indicated, this invasion has two important ecological effects. First, as in Knowler and Barbier [2000], the *ecological growth effect* reflects the fact that the population dynamics of the resident species is structurally altered by the establishment of the invader species (farmed salmon) X^F . This effect hence indicates the extent to which the growth function is negatively affected by crossbreeding (gene flow), destruction of breeding nests, and competition for food due to the invasion (see Lura [1990], Hindar et al. [1991], Lura and Sægrov [1991], Fleming et al. [2000], McGinnity et al. [2003]). The *ecological level effect*, on the other hand, reflects the fact that *EFs* add to the wild stock through a yearly influx. Knowler and Barbier [2000] analyzed a situation where the invader preys upon the resident species and hence have negative effect on recruitment. In our case, a kind of predatory behavior occurs when the *EFs* dig up wild fish spawning nests, but the *EFs* also spawn themselves. We define wild fish as all salmon that originate from river spawning. Hence, by assumption, offspring is defined as wild fish, even if recruitment may contain hybrids (cross-breedings of wild and reared salmon) and the offspring of two farmed parents.⁷

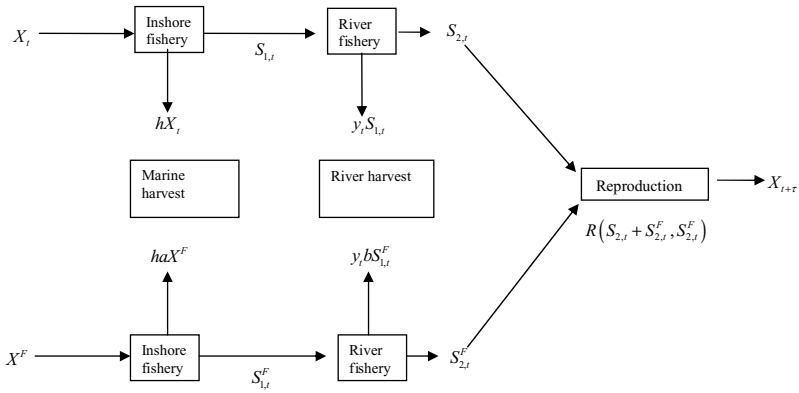


FIGURE 1. Harvest and reproduction. Wild salmon, X_t , escaped farmed salmon, X^F , marine exploitation rate, h , river exploitation rate, y_t share of escaped farmed fish available for marine and river harvest, a and b , respectively, growth function, $R(\cdot)$, time lag from recruitment to maturation age, τ .

The spawning fraction of the wild salmon stock is harvested together with the escaped farmed salmon, X^F (again, see Figure 1). However, just a proportion of the escaped fish is available to catch because the reared salmon typically starts its spawning migration later than the wild stock (Lura and Sægrov [1993], NOU [1999]). Only aX^F is therefore available in the marine fishery, where $0 \leq a \leq 1$. Accordingly, with the marine fishery harvesting fraction h_t , the escapement of reared fish from the marine harvest is $(1 - h_t)aX^F$. Therefore, the number of fish not available in the marine fishery is $(1 - a)X^F$, and the stock left over from the marine fishery is $(1 - ah_t)X^F = S_{1,t}^F$. Moreover, as most of the *EFS* enter the river after the fishing in the river is closed, only the fraction $0 \leq b \leq 1$ is available for the river sport fishery (Fiske et al. [2000]). The stock available for recreational fishing is therefore $b(1 - ah_t)X^F = bS_{1,t}^F$. Hence, with the exploitation fraction y_t , the amount $y_t bS_{1,t}^F$ is harvested in the river and $(1 - y_t)bS_{1,t}^F$ survives to be part of the spawning stock. In addition, the spawning stock includes the part of the stock that enters the river after the fishing season closes, $(1 - b)S_{1,t}^F$. The part of the stock that enters the spawning stock in the river in a given year t is therefore $(1 - by_t)S_{1,t}^F = S_{2,t}^F$. Consequently, the stock-recruitment function with *EFS* writes:

$$(1) \quad X_{t+\tau} = R(S_{2,t} + S_{2,t}^F, S_{2,t}^F).$$

The first argument in the brackets represents the above-mentioned *EFS ecological level effect*, contributing to recruitment in the same manner as the wild stock and is hence positive $\frac{\partial R}{\partial(S_{2,t} + S_{2,t}^F)} = R'_1 \geq 0$. The *ecological growth effect* in the recruitment function is indicated by the second term and is negative, $R'_2 < 0$. Notice that this differs from Knowler and Barbier [2000], who considered a constant structural shift, whereas we consider a marginal effect from the *EFS*.

3. The ecological equilibrium. In the remainder of the paper, we focus on an equilibrium model, rather than the dynamic forces, because our main goal is to establish the driving forces that follow an invasion. The time subscript is henceforth omitted⁸. Although we do not claim that the dynamic forces are negligible, the gain in analytical tractability from neglecting the dynamic forces hopefully offsets the loss of details in regard to the short-term dynamics⁹.

Following the approach by Anderson (1983, 1993), McConnell and Sutinen [1979], and Lee [1996], the recreational fishing effort is measured in terms of the number of daily fishing permits sold¹⁰. In real life, fishing permits may be for 1 day, 1 week, or a whole season, but as in Skonhøft and Logstein [2003], we collapse these possibilities into 1-day permits because this is the most common type. The fishing effort is thus expressed in terms of the number of day permits, D . We assume the catch in the river to follow the instantaneous Schaefer-type harvest function. Hence, the river yield is written as

$$(2) \quad Y = qD (S_1 + bS_1^F),$$

where Y is the total catch and q is the catchability coefficient while the content in the bracket is the total biomass available in the recreational fishery (see above). Moreover, we have that the total catch in the river per definition writes

$$(3) \quad Y = y (S_1 + bS_1^F).$$

Therefore, from equations (2) and (3) it follows that the river exploitation rate is $y = qD$. For a given marine harvest rate h , the equilibrium

version of equation (1) may then be written as

$$\begin{aligned}
 (4) \quad X &= R(S_2 + S_2^F, S_2^F) \\
 &= R((1 - qD)S_1 + (1 - bqD)S_1^F, (1 - bqD)S_1^F) \\
 &= R((1 - qD)(1 - h)X \\
 &\quad + (1 - bqD)(1 - ah)X^F, (1 - bqD)(1 - ah)X^F).
 \end{aligned}$$

For $X^F \geq 0$, we find $\frac{dD}{dX} = \frac{1 - R'_1(1 - qD)(1 - h)}{-R'_1q[(1 - h)X + b(1 - ah)X^F] - R'_2bq(1 - ah)X^F}$. In the following, we will compare the $X^F = 0$ with the $X^F > 0$ case. When first considering the case with no influx of *EFs*, it is seen that $\frac{dD}{dX} < 0$ when $R'_1(1 - qD)(1 - h) < 1$. As this is assumed to hold (see numerical section), we hence find that the biological equilibrium condition is downward sloping in the $X - D$ plane. See Figure 2. Therefore, in line with intuition, more effort means a smaller equilibrium wild salmon stock. With $X^F > 0$, we have to take into account the additional negative *ecological growth effect* working through the denominator term $R'_2bq(1 - ah)X^F$. If strong, we may find that the denominator is positive and the biological equilibrium condition is hence positively sloped. More effort then reduces the invasive stock through the negative growth effect of the invasion and eventually leads to an overall positive stock effect. However, as demonstrated in the numerical section, this effect is likely to be dominated by the term related to the *ecological level effect* ($-R'_1q[(1 - h)X + b(1 - ah)X^F]$). This yields a negative denominator but less negative than without *EFs*. As a consequence, the ecological equilibrium condition will typically be more negatively sloped than when $X^F = 0$ (Figure 2).

The effect of *EFs* may also be studied by looking at how the equilibrium schedule shifts for a given stock or effort level. For a given effort level, we find $\frac{\partial X}{\partial X^F} = [R'_1 + R'_2](1 - bqD)(1 - ah)$. Not surprisingly, the sign is ambiguous as the positive R'_1 is counterbalanced by the negative R'_2 . The ecological equilibrium condition may then shift either inward or outward due to an invasion. The intuition is clear cut as the *ecological level effect* means that more salmon are compatible with a given effort level, simply because more salmon enter the river. The *ecological growth effect*, on the other hand, has the opposite effect

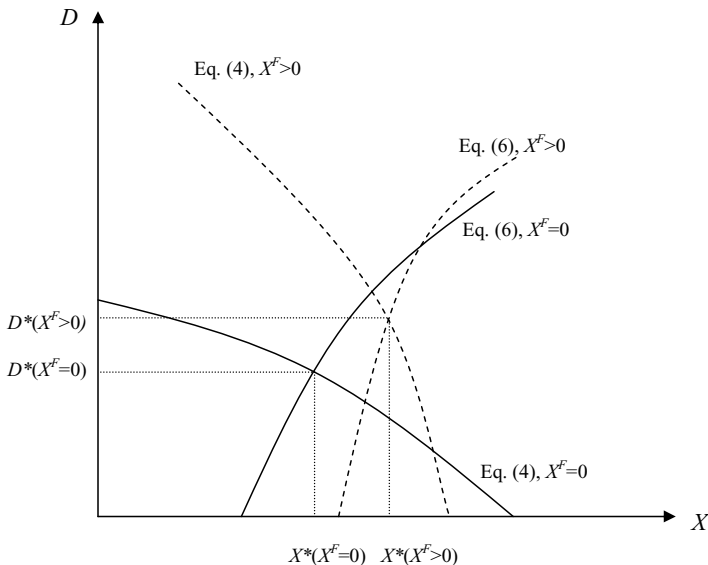


FIGURE 2. Bioeconomic equilibrium. Preinvasion (initial) state, $X^F = 0$: The curves depict the ecological equilibrium and economic equilibrium equations. Bioeconomic equilibrium is given by $X^*(X^F = 0)$ and $D^*(X^F = 0)$. Postinvasion state $X^F > 0$: The curves describe the ecological and economic equilibrium conditions with $X^F > 0$. Bioeconomic equilibrium is given by $X^*(X^F > 0)$ and $D^*(X^F > 0)$.

as the salmon stock, *ceteris paribus*, becomes less productive. Figure 2 yields the situation where the *ecological level effect* dominates for a small stock size X , and *vice versa*. However, it follows from the ambiguous effects discussed above that a situation where the ecological equilibrium schedule shifts either inward or outward for all effort levels cannot be ruled out. The implications of these potential outcomes could simply be analyzed by ignoring either the *growth* or the *level* effect. In either case, the bioeconomic outcome of an invasion with respect to stock size and effort may still be ambiguous as will become clear from the discussion below. See also the numerical section.

4. The economic and bioeconomic equilibria. We now turn to the economic part of the model. Starting with demand, this is a

question about what recreational anglers look for in the fishing experience. The price of the fishing license and the number of fishing days are expected to be important. In addition, as Anderson [1983], among others, emphasized, the average size of the fish caught, the total amount of fishing effort by all individuals, the anglers' income, the market price of fish, companions, and the nature of the surroundings may also play a role. However, empirical evidence shows that two of the most important factors affecting the demand in the Norwegian Atlantic salmon fishery are the price of permits and the fish abundance (Fiske and Aas [2001])¹¹. In what follows, only these two demand factors are taken into account but with the two above mentioned *EFS* economic effects added. The inverse market demand function in the actual river is hence a function of the number of fishing permits, in addition to the size of the wild and the *EFS* stock, and is written:

$$(5) \quad P = P \left(D, S_1 + bS_1^F, \frac{bS_1^F}{S_1 + bS_1^F} \right) \\ = P \left(D, (1-h)X + b(1-ah)X^F, \frac{b(1-ah)X^F}{(1-h)X + b(1-ah)X^F} \right).$$

The inverse demand schedule is downward sloping in the number of fishing days as the willingness to pay for the fishing experience decreases, $\frac{\partial P}{\partial D} = P'_1 < 0$. On the other hand, the willingness to pay for fishing permits increases, even if the fish is an *EFS*, due to the *economic quantity effect*, $P'_2 > 0$. Finally, the demand shifts down due to the negative *economic quality effect* expressed by the share of *EFS* in the stock as the fishermen prefer genetically "clean" wild fish, $P'_3 < 0$.¹² Therefore, the *economic quantity effect* means, *ceteris paribus*, that the angler always regards catching one more fish as positive, whereas the negative *economic quality effect* captures fishermen's concerns about the share of *EFS* in the stock. For a given *EFS* level, this negative effect is suspected to diminish in magnitude as the wild stock increases because the share of *EFS* in the total stock decreases; that is, $\frac{\partial P'_3}{\partial X} > 0$.

On the supply side we assume myopic, monopolistic management of the river. The traditional view is that even a very small spawning stock is able to fully replenish the river, so there is little reason for the river manager to consider the next generation stock. Because of the long time lag in recruitment (see above), the river manager knows that

recruitment does not return for many years, and this may also lead the manager to operate as a *de facto* myopic resource manager. Another possible explanation for such short-sighted behavior is that the river manager cannot control the marine fishery. The harvest in the fjords thus induces an extra source of uncertainty about future stock. Furthermore, the argument for myopic resource management seems to be even stronger in the case of *EFSS*, as *EFSS* adds to the complexity observed by the river manager with respect to the salmon stock. The monopolistic assumption means that the manager, who offers fishing permits to the recreational anglers, is able to take advantage of the downward slope of the demand curve. When $C(D)$ is the cost function in order to provide fishing permits, covering costs such as advertising, administration, and supervision, as well as the construction and maintenance of parking lots, tracks, fishing huts, and so forth, the river fishery profit is accordingly written as

$$\pi = P(D, (1 - h)X + b(1 - ah)X^F, \frac{b(1 - ah)X^F}{(1 - h)X + b(1 - ah)X^F})D - C(D).$$

The first-order condition for maximization of the monopolistic myopic resource manager treating the stock as exogenous is then

$$(6) \quad P'_1 D + P - C' = 0.$$

Equation (6) gives the number of fishing permits as a function of the fish stock and yields the economic equilibrium condition. Analogous to presentation of the ecological equilibrium above, we will compare the $X^F = 0$ with the $X^F > 0$ case. For $X^F \geq 0$, and neglecting any demand cross effects (see also numerical section), differentiation yields

$$\frac{dD}{dX} = \frac{-P'_2(1 - h) + P'_3 \frac{b(1 - ah)X^F(1 - h)}{((1 - h)X + b(1 - ah)X^F)^2}}{(2P'_1 + P'_1 D - C''')}.$$

The denominator is negative due to the second-order condition for the maximum. When first considering the case with no influx of *EFSS* so that $P'_3 = 0$, we find the economic equilibrium condition to be positively

sloped in the $X-D$ plane (see Figure 2). In line with intuition, more fish are then compatible with more fishing permits because demand increases. The permit sale is positive only if the willingness to pay for fishing permits exceeds the cost of providing them. Hence, there must be a certain minimum size of the stock to secure a positive supply of permits. With $X^F > 0$, the economic equilibrium condition is likely to be more positively sloped because $P'_3 < 0$. Figure 2 depicts this situation. Hence, a higher wild stock increases the demand for fishing permits more in the presence of *EF*S than without because the negative *economic quality effect* is reduced by a smaller share of invasive in the wild stock.

Although the influx of reared salmon makes the equilibrium schedule possibly steeper in the $X - D$ plane, it must also be examined in what direction this schedule shifts. For a given wild salmon stock level, we find

$$\frac{\partial D}{\partial X^F} = - \frac{P'_2 b(1 - ah) + P'_3 \frac{b(1 - ah)(1 - h)X}{((1 - h)X + b(1 - ah)X^F)^2}}{[2P'_1 + P'_1 D - C'']}.$$

Ceteris paribus, the *economic quantity effect* shifts the economic equilibrium condition upward because $P'_2 > 0$. This follows directly from the demand function because the fishing effort compatible with a given stock size increases because the yearly influx creates more demand through this effect. In addition, it indicates that the minimum stock level compatible with a positive demand decreases. On the other hand, the *economic quality effect* shifts the equilibrium condition downward because $P'_3 < 0$. Again, the explanation follows readily from the demand function as more *EF*S reduce demand through this mechanism. Which effect that dominates is an empirical question and is likely to vary from case to case, and, perhaps more important, it will depend on the initial invasion level. However, due to the demand function where the *economic quality effect* is reduced with a higher wild stock, we may suspect that this effect is more likely to dominate if the wild stock is low than high. This is also the major difference from the McConnell and Strand [1989] paper. The negative externality imposed by pollution in the McConnell and Strand paper was independent on the fish stock, but in our case, the negative externality is dependent on the wild fish

stock. Hence, a large invasion has little impact if the proportion of wild fish remains high. This new feature also means that both ecological and economic forces may pull in the direction of maintaining a high wild stock. In our case, a strong *ecological level effect* and a strong *economic quality effect* work in the direction of reducing negative stock effects of an invasion. Moreover, if the *economic quality effect* is weak or nonexistent, the economic equilibrium condition (6) shifts unambiguously upward in the $X-D$ plane due to the positive *economic quantity effect*. In economic equilibrium, a given wild stock is then accompanied by a higher harvesting effort.

The intersection between the ecological equilibrium schedule (4) and the economic equilibrium curve (6) yields the bioeconomic equilibrium. Not surprisingly, comparing the pre- and postinvasion situations, we find that in general the effects on the wild stock X and fishing effort D are both ambiguous. Figure 2 depicts the situation where both the fishing effort and wild salmon abundance increase. Hence, in this case, the *ecological level effect* and the *economic quality effect* dominate such that the new bioeconomic equilibrium is located where the ecological equilibrium schedule is shifted upward and the economic equilibrium schedule is shifted downward. Although both these effects pull in the direction of a higher wild stock, the effort effect is generally ambiguous in this situation. Hence, if the *EFS economic quality effect* is even stronger, we may have a situation where the equilibrium effort level decreases.

5. Numerical illustration.

5.1 Data and specific functional forms. The biological data used in the numerical illustration are in accordance with a typical large Atlantic salmon river in Norway, as represented by the river Orkla, located about 40 kilometer west of the city Trondheim. The Orkla River is one of the “cleanest” large salmon rivers in Norway with respect to biological invasion as the fractions of *EFS* in the catch as well as in the spawning population are relatively small. According to Fiske et al. [2000], these fractions have been around 1% and 18%, respectively (see Appendix A for a calibration of the biological model). Hvidsten et al. [2004] provide the only data available worldwide that estimate the recruitment function in a large Atlantic salmon river. They suggest the

recruitment function $R(\cdot)$ to be close to the Beverton Holt type, but that neither the Cushing nor the Ricker type recruitment can be ruled out. In what follows, we specify it as the Shepherd [1982] function, which embeds all these types of recruitment¹³:

$$(7) \quad R(S_2 + S_2^F, S_2^F) = \left[\frac{r(1 - \varepsilon(S_2^F)^\eta)(S_2 + S_2^F)}{1 + \left(\frac{(S_2 + S_2^F)}{K}\right)^\gamma} \right],$$

where $S_2 = (1 - qD)(1 - h)X$ and $S_2^F = (1 - bqD)(1 - ah)X^F$ (section 3 above).

The r is the maximum number of surviving recruits per spawning salmon, K is the stock level where density dependent mortality factors start to dominate stock independent factors¹⁴ and γ is the so-called compensation parameter measuring the degree to which density-independent effects compensate for changes in stock size. In addition, the parameter ε measures the negative *EFS* ecological impact. In the recruitment function (7), we hence find the *ecological level effect* governed by the term $(S_2 + S_2^F)$ included both in the denominator and numerator, whereas the *ecological growth effect* is governed by the single term $\varepsilon(S_2^F)^\eta$, where $\eta > 0$, in the numerator. Note that the marginal negative *ecological growth effect* is constant when $\eta = 1$, decreasing for $\eta < 1$, and increasing when $\eta > 1$. The baseline biological, as well as economic, parameter values are found in Appendix A. In the numerical simulations, we assume $\eta = 1$. ε must accordingly be calibrated such that $\varepsilon(S^F) < 1$ holds.¹⁵

The inverse demand function is specified as

$$(8) \quad P\left(D, S_1 + bS_1^F, \frac{bS_1^F}{S_1 + bS_1^F}\right) \\ = \alpha(S_1 + bS_1^F) - \beta D - w\left(\frac{(S_1^F)^\theta}{S_1 + S_1^F}\right),$$

where $S_1 = (1 - h)X$ and $S_1^F = (1 - ah)X^F$ (section 4). The choke price α gives the maximum willingness to pay when the quality-translated catch is one fish per day, whereas β reflects the price response

in a standard manner. The ambiguous demand effects following *EF**S* are easily recognized in equation (8). The demand increases through the *economic quantity effect* channeled by the term αbS_1^F . On the other hand, the demand shrinks as the proportion of farmed fish in the total stock increases through the *economic quality effect* in the last term of (8). The parameters $w \geq 0$ and $\theta > 0$ measure this effect. The cost function is finally specified as $C(D) = c_0 + cD$, where c_0 and c are the fixed and the marginal costs of providing fishing permits, respectively.

With these specifications, the number of fishing permits from the first-order condition (6) follows as

$$(9) \quad D = \frac{\left[\alpha (S_1 + bS_1^F) - c - w \frac{(bS_1^F)^\theta}{S_1 + bS_1^F} \right]}{2\beta}.$$

The preinvasion demand is found simply by setting $X^F = 0$ and thus $S_1^F = 0$. Note that although the share of *EF**S* in the stock influences demand directly, equation (9) reflects the fact that river managers do not see the fishing permit sales as an instrument to influence this share. One possible reason for this is that a very small proportion of the river catch consists of *EF**S*. On the other hand, this would be an argument for the river manager to reduce the catch in order to increase the share of wild salmon in the spawning stock. However, consistent with our assumption that the manager is myopic, the manager ignores the spawning stock, including the composition of wild and farmed spawners. Note that with $w = 0$ and no *economic quality effect* in demand, the equilibrium condition shifts unambiguously up in the X - D plane when $X^F > 0$ while the slope changes as well when $w > 0$ and $X^F > 0$.

5.2 Results.

5.2.1 *Baseline calculations.* Table 2 reports the results in the pre- and postinvasion situations with the baseline parameter values. As seen, the *EF**S* only modestly affects the stock because of the two contradictory ecological effects. Consequently, the marginal stock change is largest when the initial *EF**S* level is low. For example, this could be a situation where safety investments in the sea farming industry have reduced

TABLE 2. Pre- and postinvasion effects of *EFS* (in 1,000).

	Preinvasion	Postinvasion				
	<i>EFS</i> = 0	<i>EFS</i> = 2	<i>EFS</i> = 4	<i>EFS</i> = 6	<i>EFS</i> = 8	<i>EFS</i> = 10
<i>X</i>	12.6	13.8	14.5	14.7	14.7	14.5
<i>D</i>	3.5	3.6	3.3	2.8	2.2	1.5
<i>P</i>	0.5	0.5	0.4	0.4	0.3	0.2
<i>AS</i>	727	845	705	618	395	189
π	1,453	1,532	1,289	936	578	273
<i>TRS</i>	2,180	2,377	2,084	1,554	973	462
<i>TS</i>	2,520	2,793	2,562	2,081	1,542	1,069

Wild salmon stock *X* (in 1,000), number of day permits *D* (in 1,000), price of day permits *P* (in 1,000 NOK), Recreational angler (consumer) surplus *AS* (in 1,000 NOK), river manager profit π (in 1,000 NOK), total river surplus *TRS* (in 1,000 NOK), and total (marine and river) surplus *TS* (in 1,000 NOK). Marine harvesting rate $h = 0.30$.

the number of accidental releases, or where aquaculture is abandoned in some fjords in order to establish national farming free zones.¹⁶ In addition, the fishing effort increases when the number of *EFS* shifts from the preinvasion case, where *EFS* = 0, to the postinvasion case, where *EFS* = 2 (in 1,000), and it is almost the same as preinvasion when *EFS* = 4. However, increasing the number of *EFS* further decreases the fishing effort because of the increasing *economic quality effect*, even if the stock increases. Note also that the wild stock is not strictly increasing with an increased level of *EFS*, meaning that, given the baseline parameter values, the negative *ecological growth effect* dominates when the proportion of *EFS* reaches a certain level (*EFS* > 8).

Further, in the postinvasion situation, we find that the profit may rise because of more *EFS* through the *economic quantity effect*. Comparing *EFS* = 0 and *EFS* = 2, it is seen that the higher stock causes more fishing days, without affecting the permit price, accompanied by a higher profit. In other words, the yearly *EFS* influx may hide both the economic and the ecological consequences of the reduced wild

salmon production. Such a situation is depicted in Figure 2 where the *ecological level effect* and the *economic quality effect* dominate. Both these effects pull in the direction of a higher fish stock but the effect on the fishing permit sale is ambiguous. Figure 2 hence depicts the situation where the number of fishing permits increases as well. This is the situation found when *EFS* increases from $EFS = 0$ to $EFS = 2$ in Table 2. However, as long as the share of *EFS* in the stock matters to the anglers, a higher invasion level will increase the importance of the *economic quality effect* and hence the fishing effort and profit may fall significantly. It is seen that the angler surplus, and thus the total river surplus, follow the same pattern as the profit in Table 2. The reduced price follows directly from the negative *economic quality effect* on demand. For the baseline invasion level, which is $EFS = 6$, the *EFS* levels in the marine and river harvest are 25% and 8%, respectively, whereas 48% of the spawning stock consists of *EFS*. As discussed above, the reason for the various *EFS* levels in the different fisheries is not due to selective harvesting but simply the availability of *EFS* in the different fisheries given by the inflow fractions a and b (section 2). Hence, the main reason why the *EFS* level in the spawning stock is so high is that a larger fraction of *EFS* than wild salmon enters the rivers after the fishing season closes (Fiske et al. [2000]).

5.2.2 *No economic quality effect.* Now, we turn to a situation where the anglers consider “a fish as a fish” and the *economic quality effect* is disregarded. We hence have $w = 0$ in the inverse demand function (8) and more *EFS* translates directly into higher demand. At the same time this means that the economic equilibrium schedule unambiguously shifts up in the X - D plane in Figure 2. In this case, the salmon stock increases modestly as the number of *EFS* increases. See Table 3. In addition, both the fishing effort and permit prices increase due to the *economic quantity effect*. The results reported here hence reflect the situation where the *ecological level effect* dominates the *ecological growth effect* and where the *economic quantity effect* is not strong enough to reduce the fish stock. Thus, one problematic aspect of invasion is hidden in the absence of the *economic quality effect* in the sense that the fishing permit sale is more likely to increase. On the other hand and in line with intuition, the fish stock is always higher in the presence of the *economic quantity effect* (Tables 2 and 3).

TABLE 3. No *economic quality effect*. Pre- and postinvasion effects of *EF**S* (in 1,000).

	Preinvasion	Postinvasion				
	<i>EF</i> <i>S</i> = 0	<i>EF</i> <i>S</i> = 2	<i>EF</i> <i>S</i> = 4	<i>EF</i> <i>S</i> = 6	<i>EF</i> <i>S</i> = 8	<i>EF</i> <i>S</i> = 10
<i>X</i>	12.6	13.3	13.7	13.9	13.9	13.9
<i>D</i>	3.5	3.8	4.0	4.2	4.4	4.5
<i>P</i>	0.5	0.5	0.5	0.6	0.6	0.6
<i>AS</i>	727	871	982	1,070	1,141	1,199
π	1,453	1,741	1,964	2,141	2,282	2,397
<i>TRS</i>	2,180	2,612	2,946	3,211	3,423	3,596
<i>TS</i>	2,520	3,014	3,402	3,716	3,971	4,187

Wild salmon stock *X* (in 1,000), number of day permits *D* (in 1,000), price of day permits *P* (in 1,000 NOK), Recreational angler (consumer) surplus *AS* (in 1,000 NOK), river manager profit π (in 1,000 NOK), total river surplus *TRS* (in 1,000 NOK), and total (marine and river) surplus *TS* (in 1,000 NOK). Marine harvesting rate $h = 0.30$.

The profit, the angler surplus, and, hence, the total river surplus strictly increase as the number of *EF**S* shifts up. With *EF**S* = 6, 9% of the river catch and 71% of the spawning stock consist of farmed salmon. This means that the proportion of farmed to wild salmon in the spawning stock increases in the absence of the *economic quality effect*. However, the manner in which the concern about invasive species reduces this share through the *economic quality effect* is not straightforward. When demand is reduced because of the *economic quality effect*, the share of wild salmon in the spawning stock increases relative to the reared salmon share because the anglers mainly catch wild fish (again, recollect that this is due to the low availability of *EF**S* in the river during the fishing season, not selective harvesting). Therefore, the mechanism is not the result of any deliberate action by the anglers to decrease the share of reared fish in the spawning stock, but rather, it is a fortunate consequence of reduced demand. Again, the underlying mechanism is different from McConnell and Strand [1989] as it channels through the externality reducing effect of the wild stock.

5.2.3 *Marine fishing ban.* As mentioned in the introduction, the Atlantic salmon is harvested sequentially and where a marine fishery precedes the river harvest. Because the composition of wild and farmed salmon differs between these fisheries, changing the harvest rate in the marine fishery may influence the four effects of *EFS* discussed above. Therefore, influencing the marine fishery may be seen as a potential management tool to secure a vibrant wild Atlantic salmon stock. In the following, we therefore look at some potential results of a marine fishing ban. Note that the total surplus (TS) reported in the Tables 2–4 is the overall surplus in the marine and river fishery.

A direct result of a marine fishing ban is that more salmon enter the river and the river catch increases accordingly. For a given number of fishing days, the price of permits increases due to the increased catch per day. The fishing effort is consistently higher under a sea fishing ban than when the marine exploitation rate is positive. For example, with $EFS = 6$, the number of fishing permits D is 3.8 (in 1,000). See Table 4. In contrast, in the baseline scenario with a marine harvest

TABLE 4. No marine harvest ($h = 0$). Pre- and postinvasion effects of *EFS* (in 1,000).

	Preinvasion		Postinvasion			
	$EFS = 0$	$EFS = 2$	$EFS = 4$	$EFS = 6$	$EFS = 8$	$EFS = 10$
X	10.6	12.8	14.2	14.7	14.7	14.5
D	4.2	4.5	4.3	3.8	3.2	2.4
P	0.6	0.6	0.6	0.5	0.4	0.3
AS	1,063	1,504	1,614	1,370	967	549
π	2,127	2,409	2,187	1,731	1,194	679
TRS	3,190	3,913	3,802	3,101	2,161	1,228
TS	2,850	3,497	3,324	2,574	1,592	621

Wild salmon stock X (in 1,000), number of day permits D (in 1,000), price of day permits P (in 1,000 NOK), Recreational angler (consumer) surplus AS (in 1,000 NOK), river manager profit π (in 1,000 NOK), total river surplus TRS (in 1,000 NOK), and total (marine and river) surplus TS (in 1,000 NOK).

rate of $h = 0.3$ (Table 2), the permit sale is just 2.8. Quite intuitively, we also find that the river profit and angler surplus exceed the no-ban situation. However, when $EF\dot{S} = 6$, only 8% of the total $EF\dot{S}$ stock is fished, leaving the remaining 92% to take part in the spawning process. Hence, 57% of the spawning biomass is $EF\dot{S}$. Therefore, one unfortunate consequence of a marine fishing ban may be that the $EF\dot{S}$ level in the spawning biomass may increase (from 48% to 57% when $EF\dot{S} = 6$). Note also that even if total river surplus (TRS) exceeds the surplus without a marine fishing ban for all levels of $EF\dot{S}$ (Table 2 and Table 4), this definitely not happens for the TS: the sum of the marine and river surplus. In fact, as reported in Table 4, the opposite is true for a $EF\dot{S}$ number above that of 8. The reason for this is twofold. First, the direct loss due to the large number of $EF\dot{S}$ that is never harvested (because of the low share available for recreational catch) is high. Second, the *economic quality effect* becomes strong because a larger fraction of $EF\dot{S}$ takes part in spawning. Hence, the increasing demand due to the marine fishing ban is not enough to compensate for the loss in the marine fishery when $EF\dot{S}$ levels are high.

6. Concluding remarks. The paper demonstrates four different mechanisms that may be important when escaped reared species mix with their wild congeners, and thereby, we reveal some important policy implications. Our results indicate that, even if the natural growth of the wild species is reduced, the total stock may increase when there is an ecological invasion. Hence, measures to reduce an invasion may very well reduce the overall river surplus because less biomass will be available for fishing. One interesting result is that, if there is no *economic quality effect*, the harvesting effort will be higher due to the *economic quantity effect* and, hence, the wild stock will be less than before the invasion. In this case, the river profit and the angler surplus will always be higher *ex post* the invasion, and both will increase with invasion of the farmed species. Thus, one consequence that follows directly from the analysis is that reporting the share of invasive species in an ecosystem may reduce the demand for harvesting the wild species. This will in turn increase the wild stock and depending on the composition of the catch, the share of resident species in the ecosystem may increase. Finally, the effect on both overall river surplus as well as TS (marine and river surplus) of shutting down the marine harvest

activity in the case of an invasion is generally ambiguous because the share of the invasive species in the spawning population (or ecosystem) may increase.

The various mechanisms discussed in the paper may be transferable to other situations where escaped farmed animals mix with their wild congeners or where an ecosystem, for any reason, faces a yearly influx of invasive species. For example, there is an apparent analogue to agricultural invaders that are grown commercially but escapes to interbreed with wild plants. The increasing aquaculture production of both salmon and other species worldwide highlights the importance of addressing this specific issue. We have demonstrated that, even taking invasive damage into account, the overall river surplus may rise following an invasion. Of course, this may have implications for incentives to reduce the accidental releases of farmed species. As shown, participants in the harvest may want invasions to persist. Perhaps more importantly, these economic forces, or lack of incentives, may explain why policy-makers must intervene if they want to reduce invasions. On the other hand, one interesting extension of the model developed here is to incorporate a social planner managing the marine and recreational fishery as well as the fish farms in a unified way. As indicated by the present analysis, the outcomes of such a planning model with respect to, say, overall river surplus and share of invasive in the spawning stock are far from clear. Making the model more realistic by including the spread of diseases and stochastic elements, and by taking existence value more explicitly into account, may alter some of the results. Nevertheless, the general driving forces described in the paper offer some general insights into the bioeconomics of ecological invasions.

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APPENDIX A

Data and calibration

TABLE A1. Baseline values prices and costs, ecological and other parameters.

Parameter	Parameter description	Value*
r	Maximum net recruitment per spawning salmon	13.5 (smolt per spawning salmon)
γ	Decides to which extent density independent factors compensates for stock changes	1.06
K	Stock level where density-dependent mortality dominates density independent factors	1,489 (number of spawning salmon)
α	Reservation price when catch per day is 1	500 ((NOK/salmon)/day)
β	Price effect demand	0.12 (NOK/day ²)
c	Marginal cost fishing permit sale	50 (NOK/day)
c_0	Fixed cost fishing permit sale	0 (NOK)
q	Catchability coefficient	0.0002 (1/day)
h	Marine exploitation rate	0.3
p	Marine net gain	90 (NOK/salmon)
y	River exploitation rate	0.58
X^P	Invasive yearly influx	6,000 (salmon)
ε	Negative impact recruitment by invasive	0.00001 (1/salmon)
η	Decides if the negative marginal ecological growth effect of <i>EFIS</i> is increasing, decreasing or constant	1
a	Share of invasive available for marine fishery	0.8
b	Share of invasive available for river fishery	0.2
w	Price effect share of invasive	0.21 (NOK/day)
θ	Decides if the negative marginal price effect of share of invasive is increasing, decreasing or constant	2

*Sources: Biological baseline values are based on Hvidsten et al. [2004] and Statistics Norway [2004]. The biological impacts of *EFIS* are based on Fleming et al. [2000] and McGinnity et al. [2003]. The economic baseline values are based on Skonhoft and Logstein [2003] and Olausen and Skonhoft [2005]. The economic effects of *EFIS* are based on Olausen [2008].

ENDNOTES

1. Note that we restrict the analysis to consider the effects of escaped farmed salmon in the recreational river fishery. From an overall welfare perspective, escaped farmed salmon may essentially be seen as a transfer from farm owners to river owners. One straightforward interpretation of neglecting the loss to farm owners is that it equals the costs of improved retention measures.

2. More generally, this effect reflects all situations in which the invasive species is connected to a harvest value.

3. Note that in the case where genetic differences between native and alien species are high, as for example in Knowler and Barbier [2000], crossbreeding is not an option, and hence, the *ecological growth effect* owes to other factors influencing growth negatively. However, there may still be an analogue to the *ecological level effect* if the invasive species is exposed to harvesting.

4. See Clark [1976] for an analysis of the dynamics of a delay-difference recruitment model.

5. Hvidsten et al. [2004] find that only 0.3%–3.8% of the spawners survive justifying this simplifying assumption.

6. Knowler and Barbier [2005] analyze a case where the annual population of the invader is stochastic. See also Olson and Roy [2002].

7. In doing so, we neglect one aspect of biological invasion because the negative effect on the gene flow due to inbreeding will continue in the next generation (Fleming et al. [2000]). However, this influence on the wild fish population is partly taken into account by the structural shift through the *ecological growth effect*.

8. For the same reason, the marine exploitation rate h is kept in the background, entering the model exogenously.

9. See for example, Olausson and Skonhoft [2008] for a dynamic analysis of a recreational fishery.

10. Another approach is found in for instance Bishop and Samples [1980], Cook and McGaw [1996], and Laukkanen [2001] who use the actual catch.

11. In a survey of Norwegian rivers, 92% of sport fishermen reported that the quality of the river in terms of average catch per day was important. In addition, 72% reported that the price of fishing permits was important (Fiske and Aas [2001]).

12. One of the required attributes of a fishing experience may be that the fish are wild. When the reported share of *EFIS* in the stock is high, the likelihood of any catch being a farmed salmon is higher. Given that the anglers prefer the genetically “clean” wild fish, a greater *EFIS*-share may reduce their willingness to pay for the fishing experience. This effect may originate from a concern about the state of a specific river’s salmon stock, or simply from the fishermen’s self-interested regard to their own catch, or both. However, the cause is of minor importance here, as the main point is to establish that the *economic quality effect* is negative.

13. The Shepherd function gives the Cushing recruitment function when $\gamma < 1$, the Beverton Holt function when $\gamma = 1$, and the Ricker function when $\gamma > 1$.

14. Note that the numbers reported in Hvidsten et al. [2004] are measured as recruits per egg per square metre. However, they are translated into the corresponding number of recruits per spawning salmon in the river (available on request).

15. Fleming et al. [2000] show in a controlled experiment that the productivity of the natives are depressed by 30% when the share of farmed to natives in the spawning population were 57%. However, if there is an increasing or decreasing marginal negative impact is not analyzed as it is a one-shot experiment.

16. The Norwegian government imposed this regulation on some fjords in 2003. The fjord where the river Orkla runs out (Trondheimsfjorden) was one of these farming free zones. However, the influx of *EFS* continuous from fish farms outside the farming free zones.

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